COMPLEXITIES OF MIGRATION: A REVIEW
With Original Data from Arizona

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The ancient riddle of bird migration continues to fascinate and baffle ornithologists. New techniques—cooperative color-banding, telescopic observations, artificial transportation of marked birds, and the use of airplanes, radar, and automatic recording devices—have come to supplement the time-honored ones, yet the riddle remains unsolved. Birds show every conceivable sort of migration behavior. Some—for example certain American quail—appear to be strictly non-migratory or resident. Others—notably the Arctic Tern (*Sterna paradisaea*), certain Golden Plovers of the genus *Pluvialis*, the Wilson's Petrel (*Oceanites oceanicus*), and the two remarkable cuckoos, *Chalcites l. lucidus* (Fell, 1947) and "*Urodynamis*" *taitensis*, which breed in New Zealand and winter on remote islands in the vast Pacific Ocean—are famous for their long-distance migrations. The continued and widespread interest in bird migration is reflected in the reprinting, with some revision, of the excellent short survey of the subject by Thomson (1949).

A growing body of evidence indicates that some long migrations are performed in a few long flights or even in a single flight. This is true mainly of water birds (notably certain geese and shorebirds), but also of some Old World landbirds such as the Needle-tailed Swift (*Hirundapus c. caudacutus*), Red-backed Shrike (*Lanius collurio*), and Black-headed Bunting (*Emberiza melanocephala*) (Stresemann, 1944a, 1944b). Among North American birds not commonly recorded between their breeding and winter ranges, and therefore possibly non-stop migrants, are the Western Grebe (*Aechmophorus occidentalis*), Black Swift ("*Nephoecetes*" *niger*), Purple Martin (*Progne subis*), Gray Vireo (*Vireo vicinior*), and House Wren (*Troglodytes aëdon*). We have a very great deal to learn about migration. Such birds as most geese of the genus *Chen*; the two small forms of *Branta—minima* and *hutchinsii*; the Whooping Crane (*Grus americana*); and the Kirtland's Warbler (*Dendroica kirtlandii*) are known or believed to have very restricted breeding ranges, yet the migrations of even these forms will not be understood without long and intensive study.

For some years, and primarily from the standpoint of season and taxonomy, I have been much interested in the migrations of birds in Arizona and other inland parts of our Southwest. My studies indicate that some of the older theories of migration, advanced to explain limited data then available, must be carefully reviewed before they achieve the status of dogma. In this paper I purpose to describe some of these migrations in the Southwest and to discuss their relation to bird migration in general.

Regularity of Migration

The most impressive aspect of present-day bird migration is, of course, its regularity in time and space. Many birds are astonishingly regular in their seasonal comings and goings. But it is not correct to think of waxwings and certain boreal finches and birds of prey as the only irregular migrants. In southern Arizona, the movements of various thrushes, some fringillids—notably the Lawrence's Goldfinch (*Spinus lawrencei*)—some corvids, the Lewis Woodpecker (*Asyndesmus lewis*), the Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*), and probably some sandpipers and the Sprague's Pipit (*Anthus spraguei*), are very erratic. Furthermore, banded individuals of supposedly rather regular species of owls and ducks have made long journeys in quite unexpected directions.

Except for species such as those just mentioned, and others which are extending their ranges, most small birds are extremely regular in their migrations, not varying greatly from year to year in date, route, or abundance. In the Southwest this is true of cuckoos, goatsuckers, swifts, hummingbirds, woodpeckers, and most perching birds. Physiologists now agree that the urge to migrate ("*Zugdisposition*") originates most probably in the cycle of activity of the anterior

lobe of the pituitary gland (see the recent summary by Farner, 1950). This must be a very precise cycle, though the actual migration may be stimulated by weather patterns, as reviewed in a recent issue of *The Wilson Bulletin* (Bagg *et al.*, 1950). The general regularity of migration extends even to such peculiar cases of partial migration as those reported for smaller British birds (Lack, 1943–1944); to birds rather sedentary in some northern parts of their ranges but strongly migratory in other northern parts, e.g., the Turkey Vulture (*Cathartes aura*), Brown Creeper (*Certhia familiaris*), Mockingbird (*Mimus polyglottos*), and Golden-crowned Kinglet (*Regulus regulus*); to birds in which migration varies, in time or extent, with age and sex, e.g., certain shorebirds, the Costa's Hummingbird (*Calypte costae*), Yellow-headed Blackbird (*X. xanthocephalus*), and Western Tanager (*Piranga ludoviciana*); and to birds which migrate in different ways—in flocks, family groups, or singly; by day or by night; feeding or fasting as they go.

Complications are shown by the hummingbirds of Arizona. Not only does each species occur in a particular season and range, but within the species the season of occurrence of adult males is often different from that of females and young. The route in spring may be different from, or more restricted than, that in fall. Deelder (1949) found that female Scandinavian Chaffinches (*Fringilla c. coelebs*) migrated earlier, farther, and by a different route from, the males. How can such complexities be explained on a simple basis of temperature, food supply, or photoperiodicity?

Historical and Ecological Basis for Migration

Evidence of the historical and ecological basis of some migrations is the similarity of pattern among unrelated species. In North America several short-distance migrants from the north make their southernmost penetration in the Great Plains and Rocky Mountain regions, and fall off in numbers and extent toward both coasts southwardly. Such birds include the Rough-legged Hawk (*Buteo lagopus*); the larger races of Horned Lark, *Eremophila a. alpestris*, *E. a. hoyti*, and *E. a. arcticola*; the Northern Shrike (*Lanius excubitor*); Tree Sparrow (*Spizella arborea*); Lapland Longspur (*Calcarius lapponicus*); and Snow Bunting (*Plectrophenax nivalis*). In this same area, migration away from lowland breeding grounds tends to be the rule—particularly among ground-feeding birds like the Turkey Vulture, Mourning Dove (*Zenaidura macroura*), Mockingbird, Loggerhead Shrike (*Lanius ludovicianus*), Cowbird (*Molothrus ater*), and Rufous-crowned, Field, and Song Sparrows (*Aimophila ruficeps*, *Spizella pusilla*, and *Melospiza melodia*). Correlations between migration, winter temperatures, and the depth and duration of snow-cover[1] may be seen here. On the other hand, certain tree-feeding boreal birds show considerably less tendency to migrate in the mountains of this same region than they do farther east. Red-breasted Nuthatches (*Sitta canadensis*), Brown Creepers, Winter Wrens (*Troglodytes troglodytes*), Golden-crowned Kinglets, and even jays and chickadees seem to be less migratory here than along the Atlantic seaboard.

Variation in Time of Migration Within the Species

Discussions of the migration of certain species often suffer from indiscriminate lumping of individuals and races. This can easily produce false impressions. For example, the Yellow Warbler (*Dendroica petechia*) arrives in extreme southern Arizona by mid-March, in northeastern Arizona in late April, and in Canada and Alaska in May and early June. It would, therefore, be perfectly logical to assume that these birds move northward in the manner suggested by the old theory. The theory was that migration paralleled the advance of isotherms in the spring: that the birds moved northward very slowly at first, but more rapidly each day, in keeping with the increasing tempo of the advance of spring over the continent. In this way,

[1] Snow-cover as an ecological factor has been little discussed in North America, though there is an extensive Russian literature concerning it (Formosov, 1946).

each bird was alleged to arrive on its breeding grounds, by convenient flights, just when it was ready to breed (Griscom, 1945: 92, 108). Unfortunately for this attractive theory, all March and early April Yellow Warbler specimens from Arizona are of the bright-colored southwestern race, *sonorana*, which arrives and establishes territories here long before it is ready to breed; the more northern races do not normally reach Sonora and the southwestern United States before rather late April; while the dull far northern race, *rubiginosa*, does not ordinarily enter the United States until May. This form has been taken in extreme southern Sonora as late as June 8 and 30! While it is dangerous to argue from analogy, do not these known facts about the Yellow Warbler suggest that Red-eyed Vireos (*Vireo olivaceus*) which reach the Florida Keys in early May (when the Red-eyed Vireos of the southern United States are already beginning to nest) are individuals bound for points along the northern frontier of the species' range?[2]

An example of the complexity of fall migration is provided by the Hermit Thrush (*Hylocichla guttata*). In the mountains of southern and central Arizona the large race *auduboni* nests in the fir and spruce forests of the boreal life-zones. It is joined in mid-September by migrants of the same and other southern races; during early October these range widely in the mountains and appear uncommonly in the lowlands. Practically all, both breeding race and migrants, leave for the south by late October, when they are rapidly replaced by Alaskan birds (of the nominate race). The Alaskan birds winter here at a little lower altitude (mainly in Upper Sonoran Zone chaparral) than the breeding areas of *auduboni*, which has now retired to the highlands of México and Guatemala. Thanks to the well marked and readily identifiable subspecific characters of these birds, an apparently vertical migration has been shown, by careful collecting and identification, to be actually a composite of different latitudinal migrations! Nearly all "vertical migrations" in the northern hemisphere can be equally well regarded as short southward migrations; few if any birds descend to the lowlands on the *north* side of their mountain homes in the fall. Individuals may wander in that direction, however, as seems to be indicated by the Steller's Jay (*Cyanocitta stelleri*) reported by Hough (1949).

Alleged up-mountain movements in late summer and "midsummer wandering" should be further investigated. Most birds concerned are either southbound transients or breeding birds present before the arrival of human observers. Fledged young seeking territories move about, of course, to some extent; and this may be the explanation of the Canyon Wrens (*Catherpes mexicanus*) reported by Packard (1946: 157) from high in the mountains of Colorado "in summer and autumn." [3] What is more significant, it seems to me, is that Packard does *not* list any high-altitude records of such birds as the Scrub or Woodhouse's Jay (*"Aphelocoma" coerulescens*), Mockingbird, Virginia's Warbler (*Vermivora virginiae*), Arkansas Goldfinch (*Spinus psaltria*), or Cassin's Sparrow (*Aimophila cassini*), which are near the northern limits of their ranges in this region, nor of the several sagebrush, juniper, and piñon-inhabiting species to the west. In late August and September, Marsh Hawks (*Circus cyaneus*), Sparrow Hawks (*Falco sparverius*), Mourning Doves, Arkansas Kingbirds (*Tyrannus verticalis*) and Lark Sparrows (*Chondestes grammacus*) are to be seen in virtually all unforested high parts of the western United States. Have these species moved up the mountains from their breeding grounds? Probably not. Probably they are performing a normal north-to-south migration.

The "Flyways" Concept

The three main zoogeographic divisions of the United States are bounded by the Great

[2] Svärdson (1947) reported that in 1946 the spring migration of the Wood Warbler (*Phylloscopus sibilatrix*) through Denmark and Sweden proceeded independently of isotherms. One hundred observers collaborated in the study.—Editors.

[3] This wren, however, apparently forages up and down steep hillsides for hundreds if not thousands of feet in the course of a day, and the actual distance from occupied territory is not mentioned.

Plains (at about the 100th meridian) and by the Sierra Nevada-Cascade Mountain axis. Yet even these major regions hardly deserve to be called migration "flyways". Such a term might imply, to the uninitiated, that migratory birds are found only along certain rather narrow lines. Actually, of course, migration is almost universal, though it is less conspicuous in some tropical islands, and in humid areas such as Pacific northwestern North America, than in most mid-continental areas. Concentrations of migrants do follow coast-lines, to be sure, and some species utilize thermal air-currents above hills and mountains. Waterfowl and swallows tend to follow rivers flowing north to south or south to north across arid regions. But the same species occur over wide areas away from these lines, also. Ducks are known to cross quite normally from one "flyway" to another (Aldrich *et al.*, 1949). Many North American fringillids and other land-birds do not even stay within the same major zoogeographic division while migrating. Examples include hummingbirds, thrushes, warblers, and perhaps even some such partial migrants as the Ground Dove (*Columbigallina passerina*) and Vermilion Flycatcher (*Pyrocephalus rubinus*). Ignoring our "flyways", the Catbirds (*Dumetella carolinensis*), Veeries (*Hylocichla fuscescens*), Red-eyed Vireos, and Bobolinks (*Dolichonyx oryzivorus*) of the Rocky Mountain-Great Basin region retrace the route by which, presumably, they entered that area. So do the many eastern birds now nesting in Alaska and northern British Columbia, and the Old World forms now nesting in Alaska and Greenland. Such criss-crossing of constant, regular routes at definite seasons shows the innate character of migration.

Accuracy in Orientation and Navigation

The accuracy of this innate control is remarkable. Although the vast Pacific Ocean is neither absolutely uniform nor wholly without landmarks (Preston, 1949), the annual visits of shorebirds to remote atolls southward as far as New Zealand are still amazing. Without precise orientation surely these birds would have been exterminated long since. Of special interest in this connection is the Townsend's Warbler (*Dendroica townsendi*), which has two winter ranges, separated by hundreds of miles. Some winter along the California coast from Pasadena northward to San Francisco Bay, while the rest apparently winter from central and northeastern México (Nuevo León) to El Salvador, and the species is purely casual in the extensive region intervening. The winter range of the Alaska Myrtle Warbler (*Dendroica coronata hooveri*) is similarly divided, but stragglers have been reported from the intervening territory more frequently.

A migrating bird may, after getting its bearings, continue by using visual clues; its sense of direction may function only at certain times. Thorpe (1949) divides the flight into its start, body, and termination, and points out that each part presents a separate problem. Suggested means of possible orientation are magnetic receptors (Yeagley, 1947), sensitivity to the earth's rotation (Ising, 1945), winds and air pressure patterns, and the directions of sunrise, sunset, the heavenly bodies, etc. None of these has met with general acceptance, but each may prove of some value to certain birds. We must be cautious lest we reject a theory merely because differences to be detected in stimuli are minute. Differences in time and force of sound-waves received by our two ears are also very small, yet almost without exception we instantly know the direction whence the waves have come.

At least one migratory bird, the Black-chinned Hummingbird (*Archilochus alexandri*), evidently possesses a remarkably accurate memory of the location of spots visited only once previously (Bené, 1945: 21). Visual orientation is apparently important during migration as well. In the northeastern United States, where visibility is generally limited, migrants often fly low. They can be heard calling overhead even on clear nights and they often collide with man-made obstacles of no very great height. In the clear air of Arizona, on the other hand, migrants are seldom if ever heard. This silence is not due to lack of birds. There are more species of land birds migrating in the Santa Cruz River region of southern Arizona during an average year than in more publicized areas like New York City; and only slightly fewer of

them are song-birds, which are the birds we usually hear calling as they fly overhead. The difference in proportion of song-birds is due to the relatively few species of warblers and *Hylocichla* thrushes in the west. Geyr von Schweppenburg (1949) has noted a similar silence in the Sahara Desert. This can be correlated with the range of vision in arid regions. From one western Arizona mountain it is easy to see, at dawn, mountains to the east as far distant as 135 miles, while mountains 100 miles away are usually visible all day in clear weather. Thorpe (1949) questions whether significant migrations ever occur on heavily overcast nights. Use of the eyes does not necessarily imply, however, that migrants simply see a route and learn it. Some evidence from banded birds in Europe indicates that even regular migrants may follow different routes in succeeding years (Drost, 1941).

Relation to Molt and the Sexual Cycle

The directness of the apparent correlations between migration, molt, and the sexual cycle seems doubtful. Studies of molt in relation to autumn nesting are desirable. There are genera, such as *Empidonax* and *Phylloscopus*, in which some species complete their molt before fall migration while other species, closely related, do not. In late April and May, some male warblers and sparrows taken in Arizona, hundreds of miles south of their breeding ranges, have fully developed testes; were they not fat, one would suppose they were breeding birds. Van Rossem (1945) contends that a Yellow-green Vireo, *Vireo olivaceus hypoleucus*, migrates in breeding condition through the breeding range of another race, *V. o. flavoviridis*, in Central America. Dickey and van Rossem (1938) record eggs supposed to have been laid at an overnight roost of migrating hawks in El Salvador; if, as supposed, the birds were really Swainson's Hawks (*Buteo swainsoni*), they were still well over a thousand miles south of their breeding range. McIlhenny (1932: 294) reports eggs dropped by Blue Geese (*Chen caerulescens*) just before their departure from Louisiana for the Arctic. Certain eggs found in northern Arizona do not appear to be those of any species normally nesting in the region. We know all too little about "dropped" eggs. Attention is called, too, to the fervent singing and prolonged maximum in gonad-size among Cassin's Sparrows in a region throughout which they are not known to breed (Phillips, 1944).

Various workers have recently challenged the familiar axiom that no bird ever breeds twice during the same year in different regions. It would of course require extraordinary luck and persistence, or both, to prove this. Wagner (1948) believes that Broad-tailed Hummingbirds (*Selasphorus platycercus*) which nest in the vicinity of Mexico City in autumn are the same ones that have already nested, earlier in the summer, in the Rocky Mountains of the United States. Some Arizona ornithologists have noted a post-breeding disappearance, probably a migration, from the low, hot valleys of southwestern Arizona of such birds as the Costa's Hummingbird, Say's Phoebe (*Sayornis saya*), Phainopepla (*Phainopepla nitens*), and Loggerhead Shrike. Of these, the Phainopepla is the most likely to raise a second brood elsewhere; but all are worthy of careful investigation. The casual breeding of European White Storks (*Ciconia ciconia*) in South Africa has been recorded, but this must certainly be exceptional.

Effect of Short-term Weather Influences

Accidents which happen on migration, sometimes as a result of meteorological irregularities, occasionally resolve themselves into natural experiments that may yield important clues. At the Nashville ceilometer Spofford (1949) saw birds kill themselves by flying straight into the ground when a beam of light struck them. Bishop (1949) noted the same behavior among petrels. Many of the circumstances were, of course, widely different in these two cases, and the cause is obscure in both. The great trans-Atlantic flight of Lapwings in December, 1927 (Witherby, 1928), was evidently caused by exceptional winds combined perhaps with poor visibility. But wind and rain are perfectly normal; very few storms produce remarkable flights; and an attempt to explain unusual occurrences on such a basis (Williams, 1950) may

produce conclusions which are at variance with known facts of bird distribution and migration, even if no errors of identification are involved among the "records" so explained. Weather variations have been much discussed recently by Williams (1950 and elsewhere), Bagg *et al.* (1950), Robbins (1949), Vleugel (1948), and others. Except in winter, their role is apparently merely regulatory. Seldom are migrating birds the passive playthings of the elements!

Landmarks vs. Sense of Direction

The writer does not share the optimistic opinion expressed by Griffin and Hock (1949) that many migration phenomena are explicable in terms of exploration for landmarks. Buss's observations (1946) indicate otherwise; and if Golden Plovers leaving the Bering Sea are apt to fly in *any* direction, how can we account for the extreme rarity of the entire genus in that intensively studied region to the south—the west coast of the United States, with its extensive shoreline? The Bristle-thighed Curlew (*Numenius tahitiensis*) apparently maintains an even more rigid course across the Pacific Ocean. This does not argue inefficient navigation. Neither do the observations of F. W. Loetscher, Jr., and myself on San Francisco Mountain, the highest mountain in Arizona, on July 28, 1939. There, not far below timberline, in the Inner Basin, Audubon's Warbler (*Dendroica auduboni*) is the only breeding *Dendroica*; yet during our visit we collected two of three to five Black-throated Gray Warblers (*D. nigrescens*) seen, three Hermit Warblers (*D. occidentalis*), and three Townsend's Warblers of four or five seen. The date is about the beginning of the warbler migration, especially for the last two species, which were already hundreds of miles south (or east) of their breeding grounds. An even earlier Hermit Warbler had been taken ten days before in the Santa Rita Mountains, still farther south. The important point is that every warbler observed on July 28 (as well as the Hermit Warbler taken July 18) was an immature. Within two months of hatching, these young birds had flown unerringly and unguided to the points of autumn concentration of their species! San Francisco Mountain is surrounded by a great plateau, an area superficially similar to the mountain itself, though less high of course. The forest covering the Mogollon Plateau is said to be the largest forest of yellow pine (*Pinus ponderosa*) in existence. It extends eastward as far as, and into, New Mexico. But though much more field work has been done here on the plateau, near Flagstaff, than on the mountain above, neither the Townsend's nor the Hermit Warbler has ever been found at Flagstaff before August 2, and no Townsend's before August 25. Both species are commonest in the highest forests available.

Verwey (1949) concludes that not only birds, but also fishes and aquatic mammals, have in some cases a sense of direction.

Conclusion

Is it not likely that, among the many migrations known to take place today, different kinds have arisen at different times and places, in response to different sets of conditions during geologic time? If so, how can any one set of simple theories cover all the facts? Dangerous as it may be to formulate general hypotheses on the basis of local data, we cannot ignore data simply because they do not fit widely accepted hypotheses. To be useful, a hypothesis should be flexible enough to account for quantities of local data without forcing facts to fit theories.

Migration remains a mystery, and it seems unlikely that any one simple explanation will cover any very large percentage of the known facts. The latter become stranger and stranger; readers of *The Wilson Bulletin* will recall Broley's (1947: 3–6) discovery that the Bald Eagle (*Haliaeetus leucocephalus*) is absent from Florida "during July and August." In conclusion, quoting Thomson: "What, in particular, guides the young birds in those cases where they travel apart from their parents when only a few weeks old, and yet perform a long journey in accordance with the constant pattern of their species? Therein lies the real mystery of migration."

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